Historical and contemporary influence of the Leeuwin Current on the marine biota of the southwestern Australian Continental Shelf and the Recherche Archipelago

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Abstract

The influence of the Leeuwin Current on the marine biota of the southern continental shelf of Western Australia is investigated by incorporating geological, oceanographic and evolutionary contexts. The effect of this seasonal current was found to have had an influence for approximately 40 million years as inferred from palaeontological evidence. The effect has been observed despite significant variation in the southward movement of the Leeuwin Current, sea level fluctuations, continental climate and the northward movement of the Australian continent. The marine flora and fauna of the Recherche Archipelago demonstrated the scale of the Leeuwin's reach with macroalgae, demersal fish, molluscs and other invertebrates having greater affinity with the southern temperate flora and fauna, with a small percentage of subtropical species transported eastward on the Leeuwin Current. A more detailed comparison of benthic macroalgal assemblages indicated significant differences between the Recherche, the southern temperate flora in South Australia at Isles of St Francis and the southwestern flora at Hamelin Bay, near Cape Leeuwin. These macroalgal assemblages were characterized by multiple species differences among the regions but also very high local species turnover (alpha diversity) among locations within each region. The relatively warm water and low seasonal variability in sea temperatures associated with the winter flow of the Leeuwin Current may have played a major role in the persistence of warm water species on the southern coast and the high species turnover we have observed over 18 degrees of longitude. The Leeuwin Current has played a major but not an exclusive role in the evolution and persistence of this flora as well as the species richness and endemism of other marine organisms along the southern coast of Western Australia.

Keywords: Leeuwin Current, Recherche Archipelago, southern Western Australia, evolution, macroalgae, diversity, alpha diversity

Introduction

This paper characterizes the effect of the Leeuwin Current on biota along the southern shores of Western Australia and more specifically the effect of the Current on the Recherche Archipelago. We summarize a body of literature that includes the effect of geological and contemporary processes on the biology, distribution and behavior of marine organisms found along the south coast and then more specifically for Recherche Archipelago. As a case study, the relationship that assemblages of marine macroalgae in the Recherche Archipelago have with the flora of southwest and southern Australia is then addressed. The paper then concludes with hypotheses about the potential causal mechanisms for the biogeographic relationships.

The Continental Shelf of southern Western Australia

The continental shelf off southwestern Australia extends from Israelite Bay at the western edge of the Great Australian Bight to Cape Leeuwin, covers an area of nearly 65,000 km^2 and is characterised by a 30–65 km-wide continental shelf that slopes gently to a depth of 100 m. It contrasts with the flat and gently sloping shelf of the main Great Australian Bight region east of the Recherche Archipelago (James *et al.* 1994). Further offshore, the seafloor drops away quickly after the shelf break at between 100 m and 140 m depth. In the east, the shelf is up to 65 km wide and punctuated by the granitic islands of the Recherche Archipelago (Conolly & von der Borch 1967). These islands are scattered across the entire width of the shelf and extend for more than 160 km along the coast. Sediments around the Recherche Archipelago are characterised by marine biogenic carbonates offshore and silica rich sediments onshore, that are eroded from the granites and gneisses of the archaean shield that covers a large proportion of southwestern Australia (Ryan *et al.* 2007). The shelf varies between 30 km and

65 km in width to the west of the archipelago, but most islands in the western portions of the shelf occur within 8 km of the mainland (Conolly & von der Borch 1967).

Numerous canyons incise the continental slope to the west of the Great Australian Bight. These include the Pasley and Esperance canyons offshore from the Recherche Archipelago, and the Albany Canyon Group (>30 canyons), which dissect the continental slope at regular intervals between Hood Point and Point D'Entrecasteaux (von der Borch 1968). Recent sonar surveys in the Albany Canyon Group have shown that some individual canyons are up to 2000 m deep and 90 km long, and extend uninterrupted between the shelf-break and the abyssal plain (Exon *et al.* 2005).

The southern continental shelf is heavily influenced by large, deeply abrading ocean swells that erode the shelf in depths up to 100m, with greatest abrasion of the bottom in the mid shelf region between 50 and 90 m depths (James *et al.* 1994). Contemporary sediments do not accumulate and the sediments that do accumulate are mixtures of reworked Pleistocene and recent sediments (Conolly & von der Borch 1967). An example of the scale of the effect of ocean swells on the south western continental shelf can be gleaned from Hemer (2006) who, in determining combined shear stress across the whole of the Australian continental shelf, found that in 48 metres depth off Cape Naturaliste, Western Australia, mean (maximum) wave periods recorded were 7.5 sec (15.7 sec), significant wave heights were 2.2 m (11.5 m) giving a combined benthic shear stress of 1.20 Nm^{-2} (85.9 Nm^{-2}), making it one of the highest energy sites in temperate Australia.

Palaeo-oceanography and the Leeuwin Current

The effect of the Leeuwin current or earlier proto – Leeuwin currents on water temperature and mixing of tropical species along the temperate south coast of Western Australia has been effective since the middle to late Eocene (35–42 Mya) (McGowran *et al.* 1997). Pelagic and benthic Foraminifera has been used to build a chronological palaeo-history of warm water transport southward along the west and south western coasts of Australia (Cann & Clarke 1993; Wells & Wells 1994; Mc Gowran *et al.* 1997; Li *et al.* 1999) There have been documented geological periods when the current seems to have been inactive (Early to Middle Oligocene, Early Pliocene) and reactivated (Early to Middle Miocene). The Leeuwin current strengthened in the middle to late Pleistocene and enhanced the southward transport of more tropical species (*Anadara trapezia* arcoid bivalve and *Acropora* corals) in southwest Australia and the inshore surface water temperatures during the last interglacial (122 –120 kyr BP) were > 2°C than they are today (Kendrick *et al.* 1991; McGowran *et al* 1997; Murray-Wallace *et al.* 2001). More recently during the late Quaternary, water north of 18°S varied little in temperature despite large extremes in climate, whereas further south there was significant changes to surface water temperatures, suggesting southward influence of the Leeuwin Current was disrupted during both glacial and interglacial extremes (Wells & Wells 1994).

There is a strong longitudinal temperature gradient and faunal pattern along the southern coastline of Western Australia generated by the Leeuwin Current. Larger benthic foraminifera show a west to east gradient in occurrence along the southern coast of Western Australia, with the genera *Heterostegina*, *Amphistegina*, *Amphisorus* and *Planorbulinella* common in sediments at Cape Leeuwin (115°S), *Amphistegina*, *Amphisorus* and *Planorbulinella* at Albany (117°S), and only *Amphisorus* at Esperance (122°E) (Li *et al.* 1999). At Esperance, the presence of tropical foraminifera, especially the benthic *Amphisorus* (*Marginopora*) taxon, both as living and in reworked sediments (120,000 yr BP) infer that the southward movement of the historical and contemporary Leeuwin Current has heavily influenced the benthic assemblages in this region at least since the last interglacial (Cann & Clarke 1993; Li *et al.* 1999).

As the Leeuwin Current seasonally flows during winter months and is episodic in strength of flow and influence on the south coast, it is quite amazing that it has such long geological time scale influences on benthic organisms as demonstrated for the arcoid bivalves (Kendrick *et al.* 1991) and benthic and pelagic foraminifera (Li *et al.* 1999).

The effects of sea level fluctuations and wave abrasion over the same geological period do not appear to weaken the overriding influence of the west to east gradient in the strength of the Leeuwin Current. Interestingly, Li *et al.* (1999) found the benthic foraminiferal assemblages during the late interglacial period were representative of lagoonal environments whereas recent assemblages were more representative of shallow open shelf environments.

The Contemporary Leeuwin Current on the South Coast of Western Australia

The Leeuwin Current moves eastward over the western shelf (Albany to Bremer Bay) moving offshore near the shelf break further eastward (Recherche Archipelago) and is strongest during winter. It warms sea-temperatures, and bathes the coastline with low nutrient waters. Light is generally less limiting to benthic and planktonic primary producers on the inner continental shelf and water column attenuation coefficients are very low, as water column turbidity from phytoplankton blooms and from river discharges are small (k_d = 0.08: Carruthers *et al.* 2007). The surface waters of the southwestern Australian shelf, waters of the Leeuwin Current and surface waters offshore are very low in nitrogen (less than 0.5 μmol) year round and primary productivity is nitrogen limited (Lourey *et al.* 2006).

Characteristics of Flora and Fauna on the south coast

The southwestern corner of Australia is a region of high species diversity and endemism for many marine organisms; for example, marine macroalgae (Womersley 1990; Phillips 2001), invertebrate taxa such as molluscs and echinoderms and decapod crustaceans(Wells *et al.* 2005; O'Hara & Poore 2000), and nearshore (Hutchins 1994) and continental slope demersal fish (Williams *et al.* 2001). High species richness in the region is attributed to the lack of mass extinction events associated with unfavorable environmental conditions – such as glaciation – over the recent geological past, and the moderating influence of the Leeuwin Current since the

Eocene (McGowran *et al*. 1997). The high endemism of the region is a product of long isolation of the marine flora and fauna as Australia has been separated from other land masses for the past 80 million years (Veevers 1991; Phillips 2001).

Effects of Leeuwin Current on Demersal and Migratory Fish

The Leeuwin Current is regarded as the dispersal mechanism responsible for transporting subtropical and tropic fish species southwards along the west coast (Hutchins & Pearce 1994) and eastwards along the south coast of Western Australia. The south coast of Western Australia is dominated by temperate demersal fishes that are found across the whole southern shores of Australia, although there are increasing numbers of sub tropical species from Israelite Bay to Cape Naturaliste (Hutchins 2001). Only 56% of demersal fish species are shared between the south coast, from Israelite Bay to Cape Naturaliste, and the lower west coast, Perth to Port Denison, and only 29 % with the central west coast, from Houtmans Abrolhos to Kalbarri. (Hutchins 2001). This influence is not as strong in surf zone fish assemblages. There is a decrease in total number of surf zone fish species from the west coast (20–66 species) to the south coast (11–16 species), and also a notable absence of tropical species in surf zone assemblages from the south coast (Ayvazian & Hyndes 1995).. The influence of the Leeuwin Current is also evident on recruitment and recruitment limitation. For example in pilchards (*Sardinops sagax*) along the south coast (Fletcher *et al*. 1994) there was a strong eastward transport of pilchard eggs from Albany over 150 km distances within days during winter when the Leeuwin Current was at its strongest but not during summer, resulting in geographical discontinuities in the early life histories of some populations of pilchards. This suggests that the Leeuwin Current influences fine spatial scale population structure in this highly mobile species. Interestingly, other highly mobile species are less influenced by the Leeuwin flow. The Australian herring (*Arripis georgiana*) is highly migratory and can be treated as a single stock from Victoria to southern Western Australia (Ayvazian *et al*. 2004).

Effect of the Leeuwin Current on Zooplankton

Both chaetognaths and siphonophores were better represented and more speciose during winter than summer (Gaughan & Fletcher 1997). Numbers of species decreased along 11 cross-shelf transects between Albany and Esperance in winter but not summer and this gradient reflected the decline in numbers of tropical species entrained in the Leeuwin Current during winter. The species of siphonophores and chaetognaths observed were all characteristic of warm waters and no cold temperate species were found.

Effect of the Leeuwin Current on Echinoderms and Decapod crustaceans

O'Hara & Poore (2000) analysed the distributions of 739 species of temperate Australian echinoderms and decapod crustaceans and noted that the western peak in species diversity at Perth, Western Australia, was 2 degrees further south than the eastern peak in species diversity at Sydney, New South Wales. Their interpretation of the geographical peaks in species richness should be taken with caution as it is confounded by sampling intensity and the proximity of Perth and Sydney to State and commonwealth Museum and research groups specializing in invertebrates. There were many endemic subtropical and tropical species characteristic of the lower west coast and their more southern distribution was due to the influence of the Leeuwin Current in transporting subtropical and tropical species southwards. The south coast of Western Australia from Albany to Eucla varies by only 2 degrees latitude and has a few degrees change between summer and winter water temperatures. O'Hara & Poore (2000) found relatively high species turnover, or replacement, across this region and inferred that the higher winter temperatures (Leeuwin Current) and small differences between summer and winter temperatures have allowed subtropical species to persist further east than may be expected. This results in a longitudinal turnover from more subtropical species to the west to more temperate species to the east but with little change in species richness.

Effect of the Leeuwin Current on Macroalgae

Wernberg *et al*. (2003) combined quantitative surveys of macroalgal diversity on limestone reefs from Marmion, north of Perth, Hamelin Bay and Hopetoun and concluded that there was a cline in overlapping species distributions from the west coast to the south coast. Wernberg *et al*. (2003) inferred that this cline indicated mixing of species from north to south, presumably through transport of propagules in the Leeuwin Current. They also found a shift in dominant canopy algae from the eurythermal *Ecklonia radiata* kelp forests common on the west coast to *E. radiata* combined with more southern temperate *Scytothalia doryocarpa* and *Cystophora* in the central south coast.

Influence of the contemporary Leeuwin Current on the Recherche Archipelago

The Recherche Archipelago is a group of 108 islands and many small reefs between 122°E and 124°E longitude. They are predominantly inshore on the shelf and are often not influenced by the main body of the Leeuwin Current that is situated on the outer continental shelf and slope at these longitudes. Interestingly, the Leeuwin current flows out to sea from the shelf break to the south of the eastern Recherche Archipelago, with an onshore movement of nutrient enriched sub-Antarctic waters (Cresswell & Griffin 2004). The effect of these colder nutrient-rich sub-Antarctic waters on the continental shelf near the Recherche Archipelago is unknown. Cresswell & Griffin (2004) postulate that this southward movement of the Leeuwin Current may be due to the 30° change in shelf orientation or the outflow of warmer waters from the Great Australian Bight or a combination of both. This offshore movement of the Leeuwin Current generates the strong anticyclonic eddies that develop south of the shelf break and are characteristic of waters south of the southern Western Australian continental shelf. The Recherche Archipelago is only seasonally bathed in Leeuwin Current waters and water temperatures are generally colder than offshore waters, and inshore waters to the west except for the months October and November (Figure 2 in Cresswell & Griffin 2004). Thus the overall strength of the Leeuwin Current may heavily affect the year to year influence on the biota of the Recherche Archipelago.

Floral and Faunal characteristics of the Recherche Archipelago

We first summarise the contemporary distribution of the predominant benthic biota, and demersal fish in the Recherche Archipelago. Then, using the macroalgae as an example, we investigate what makes this region interesting and how it is related to the temperate flora to the east and the subtropical and tropical flora associated with the west coast of Western Australia and the Leeuwin Current. We describe the importance of consistent ocean climate over millennia and its influence on the diversity and endemism of the macroalgal flora and incorporate both contemporary ecology and historical biogeography in the description of the effects of the Leeuwin Current on the marine benthos in this region.

Benthic Macroalgae of Recherche

Subtidal macroalgal assemblages of the Recherche Archipelago were more similar to macroalgal assemblages in South Australia and Victoria (Collings & Cheshire 1998; O'Hara 2001) than to those previouslydescribed from the west coast and the southwestern region of Western Australia (Wernberg *et al.* 2003). Two hundred and forty two species have been recorded in the Recherche Archipelago, with 148 species of Rhodophyta, 65 species of Phaeophyceae, and 29 species of Chlorophyta (Goldberg & Kendrick 2005) (Table 1). Range extensions were recorded for 37 species, 28 were westward extensions from the temperate southern coast of Australia and 9 were eastern extensions from southern and western shores of Western Australia west of the Archipelago (Goldberg & Kendrick 2005). This demonstrates the temperate nature of algal assemblages in the Recherche Archipelago and also our poor knowledge of the marine flora along southern Western Australia.

Marine Fauna of the Recherche Archipelago

Hutchins (2005) found the nearshore demersal fish fauna of the Recherche Archipelago totalled 263 species, with 68 species found only in Western Australia (Table 1). A barrier to eastward species dispersal was postulated to exist at the western side of the Great Australian Bight. Wells *et al.* (2005) identified 347 species of molluscs from the Recherche Archipelago, 275 were temperate southern Australian and 56 were Western Australian in distribution (Table 1). McDonald & Marsh (2005) describe 12 seastars from the Recherche Archipelago, all but one with a temperate southern distribution (Table 1). Similarly, of the 6 ascidians identified from Recherche, all had temperate southern distributions (McDonald 2005). Seventy seven hydroids were recently described from the Recherche Archipelago, 6 new species only known from the Archipelago, 58 with southern temperate distributions and only 5 restricted to Western Australia (Watson 2005). Pycnogonids have more west coast species (6) than southern temperate (5) and 1 new species only known from the Recherche Archipelago (Bamber 2005), although this trend has more to do with the geographical sampling done by the expert than the realised distributions of pycnogonids.

In summary, the marine flora and fauna of the Recherche Archipelago are predominantly temperate southern Australian in affinity. There are few species that have west coast distributions, supporting the model that the Recherche Archipelago is less influenced by the Leeuwin Current. Interestingly, the Leeuwin Current may still act as a barrier to western transport of southern Australian temperate species. This requires further investigation.

Relationship of the macroalgal flora of Recherche Archipelago with Hamelin Bay, WA and the Isles of St Francis, South Australia

Our objective was to test if the marine flora of the Recherche Archipelago (RA) was similar to that of representative floras of the south west flora documented at Hamelin Bay, Western Australia or the southern Australian flora east of the Great Australian Bight, from the Isles of St Francis, near Ceduna, South Australia. Rather than a full biogeographical analysis like that of O'Hara & Poore (2000), we have focused in on specific localities that are representative of the south western region (Wernberg *et al.* 2003; Kendrick *et al.* 2004; Toohey *et al.* 2007) and the southern region, east of the Great Australian Bight (Womersley & Baldock 2003). This decision was made because floristic sampling along the southern shores of Western Australia have been limited to a few field surveys and the taxonomic data from

Table 1

Description of the species richness and relationships of selected groups of the flora and fauna of the Recherche Archipelago with western and southern temperate Australia.

Taxon	Recherche Species Richness	Only known from Recherche	Southern Temperate Australia	Western Australia	Author
Seaweeds	234	0	186	17	Goldberg & Kendrick 2005
Fish	263	0	189	68	Hutchins 2005
Molluscs	347	0	275	56	Wells *et al.* 2005
Sea stars	12	0	11	1	McDonald & Marsh 2005
Ascidians	6	0	6	0	McDonald 2005
Hydroids	77	6	58	5	Watson 2005
Pycnogonids	15	1	5	6	Bamber 2005

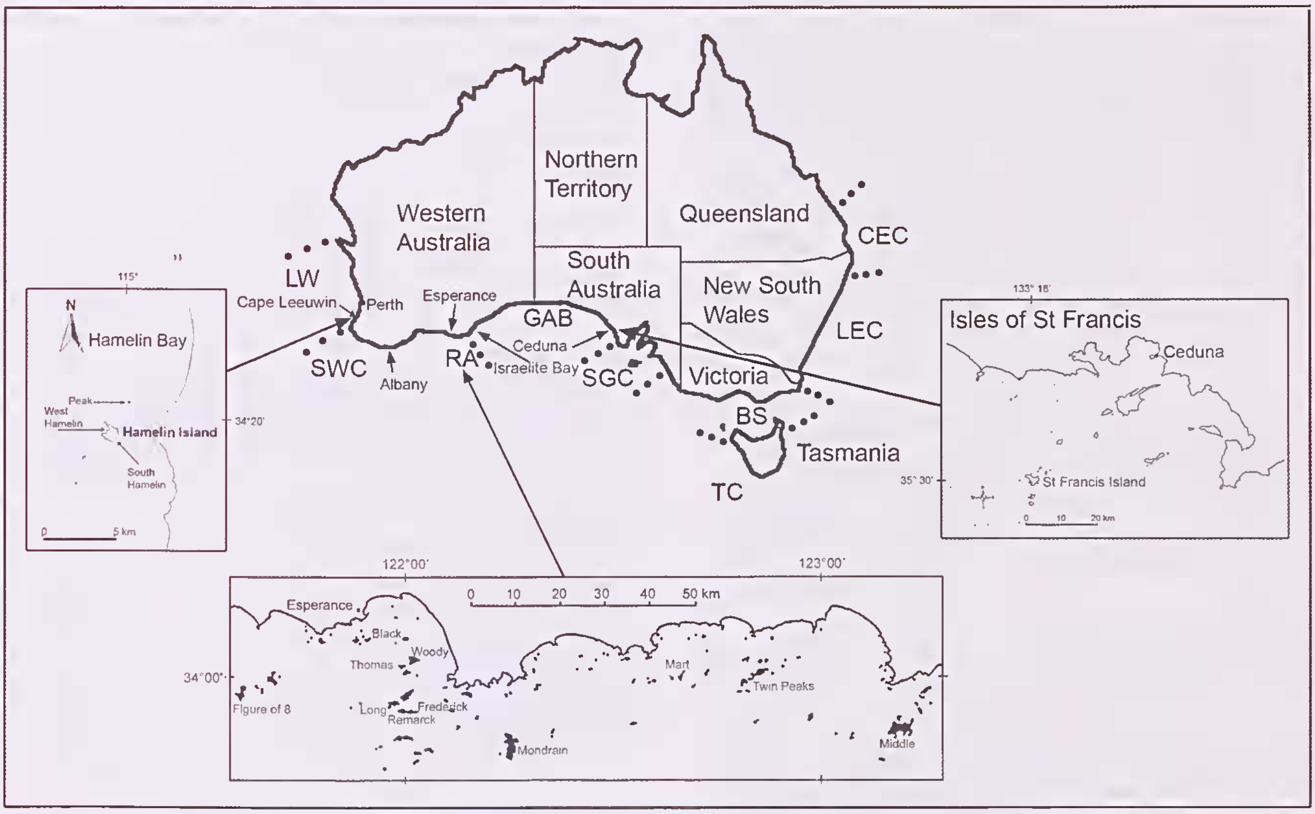

Figure 1. A. Map of Australia showing locations mentioned in the text and the CONCOM marine biogeographic regions LWC = Lower West Coast, SWC = South West Coast, GAB = Great Australian Bight, SGC = South Gulfs Coast, BS = Bass Strait, TC = Tasmanian Coast, LEC = Lower East Coast, and CEC = Central East Coast and the Recherche Archipelago (RA), with inset maps of the three study locations: Hamelin Bay, Recherche Archipelago and Isles of St Francis.

opportunistic collections, many from the drift on beaches (see Womersley 1984, 1987, 1994, 1996, 1998, 2003)

Species presence information for macroalgae for the south west flora were taken from collections made in 2006 from 18 locations in Hamelin Bay (n = 54 x 0.25 m^2 quadrats) (Figure 1) . This is part of a 6 year temporal study described in Kendrick *et al.* (2004) and Toohey *et al.* (2007). The Recherche Archipelago flora was compiled from surveys of 11 islands (Figure 1) conducted in October of 2003 and 2004 (n = 372 x 0.25 m^2 quadrats) (Goldberg & Kendrick 2004; Goldberg *et al.* 2006). Similar species data was taken from a survey of the Isles of St Francis from 12 locations (Figure 1) by Womersley & Baldock (2003). These data differ from the other locations as they are not quadrat samples but actual species lists from each location.

Multivariate tools were used to illustrate differences among floras in the southern coast of Australia. Non-metric multidimensional scaling (MDS) was used on a Bray-Curtis similarity matrix of species presence/absence data, equivalent to a Sorenson coefficient, from all three regions (PRIMER Vers. 6). A one-way permanova tested the significance of differences in macroalgal assemblages among Isles of St Francis, Recherche and Hamelin Bay (Anderson 2001). A similarity percentages analysis was conducted to assess the average similarity within versus among regions.

We found all three regions separated clearly in two dimensions on the MDS plot (Figure 2). They did not form a cline as demonstrated by Wernberg *et al.* (2003) for the south western algal flora, but were distinct groupings. Both Hamelin Bay (SW) and the Recherche Archipelago (RECH) formed tight clusters whereas the locations from the Isles of St Francis (FRANCIS) were more dispersed. This difference was possibly driven by the difference in sampling intensity between regions; Isles of St Francis were qualitative species lists made from collections at locations whereas both Recherche and Hamelin Bay were quantitative samples taken using quadrats. The permanova on species presence/absence (Table 2) and pairwise tests between regions (Table 3) demonstrated that macroalgal assemblages in all 3 regions were highly significantly different.

The average similarity accounted for by among and within regions demonstrates some overlap in species presence/absence among regions (Table 4). The macroalgal assemblage in Hamelin Bay (SW) shared almost 25% with the Recherche Archipelago (RECH) but only 14% with the Isles of St Francis (FRANCIS). The Recherche Archipelago shared approximately 21% with the Isles of St Francis. Clearly, these flora are not that similar among regions. What is driving this difference? The shared similarity among locations with regions also is small (diagonals in Table 4). Locations within regions shared less than 50% of species for both Hamelin Bay and the Recherche Archipelago. From the species lists from the Isles of St Francis it was less than 22%. Clearly the macroalgal flora within each region shows high levels

Table 2

One- Factor Permanova comparing species presence macroalgal assemblage data from the 3 regions (Hamelin Bay, Recherche Archipelago and the Isles of St Francis) along the south western and central coast of Australia.

Source	df	MS	Pseudo-F	P(perm)
Regions	2	16243	8.8009	0.0001
Residual	41	1845.6		
Total	43			

Table 3

Pairwise comparisons between Hamelin Bay (SW), the Recherche Archipelago (RECH) and the Isles of St Francis (FRANCIS).

Groups	t	P(perm)	perms
SW, RECH	3.3896	0.0001	9872
SW, FRANCIS	2.2909	0.0001	7661
RECH, FRANCIS	3.0584	0.0001	9912

Table 4

A matrix of the average similarity of macroalgal assemblages within and among regions along the south western and central coast of Australia. SW = Hamelin Bay, RECH = Recherche Archipelago, FRANCIS = Isles of St Francis)

	SW	RECH	FRANCIS
SW	*48.71*		
RECH	24.96	*48.43*	
FRANCIS	14.40	20.61	*21.88*

of species turnover among locations. The species responsible for the differences among and within regions were many with no species contributing more than 1.6 % to the overall percentage of dissimilarity among the regions.

Discussion

The macroalgal flora and fauna of the Recherche Archipelago is more similar to the temperate flora found along southern shores of Australia. Separation of the south coast of Australia from Antarctica began approximately 90 million years ago and ended 30 million years ago with oceanic water flowing between the two continents (Poore 1994). During this period of separation between Australia and Antarctica, the macroalgal flora in the shared waters between the two continents was presumably Tethyan in origin (Phillips 2001). Clayton (1994) speculated that prior to formation of sheet-ice, Antarctic macroalgal species richness was similar to that of temperate southern Australia, particularly for species in the Phaeophycean order Fucales (*e.g.*, *Cystophora* and *Sargassum* species). Coastal sea temperatures have remained temperate as the continent moved with the northerly drift of the Australian plate, with a warm-water influx from the Leeuwin Current along the west coast (Phillips 2001). This has resulted in southward and eastward transport of subtropical species from central and northern Western Australia. These subtropical species are a small percentage of the predominantly temperate flora and fauna found in the Recherche Archipelago.

Species replacement (turnover) of the marine macroalgae from east to west along the southern shores of southwestern Australia is great, although, species

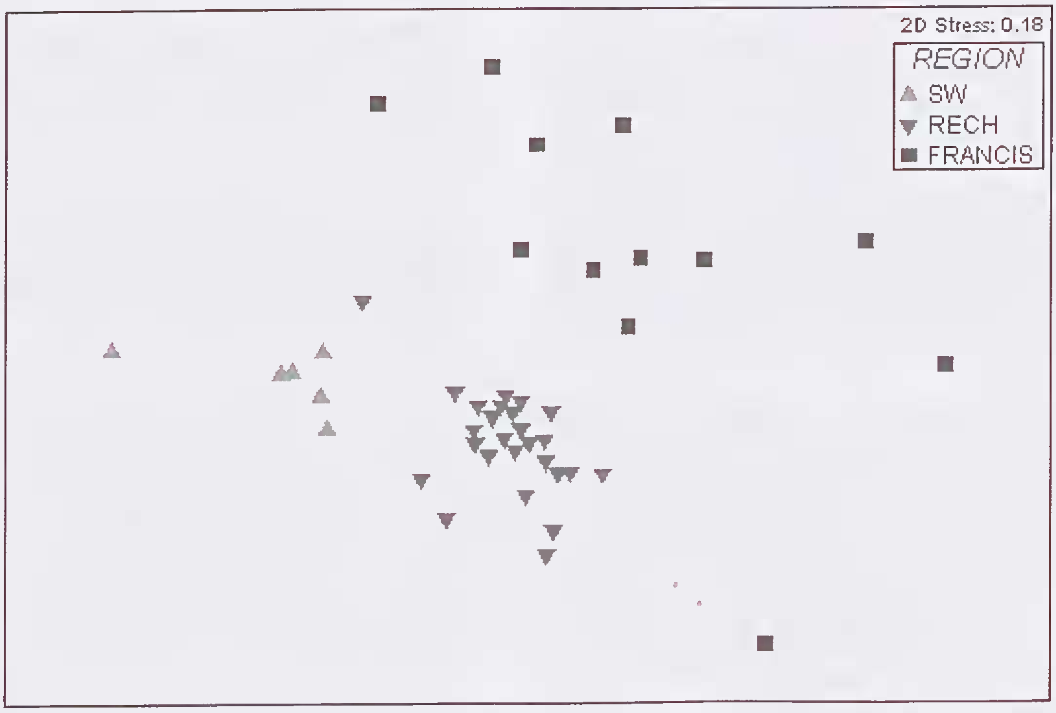

Figure 2. Non-metric two-dimensional multidimensional scaling plot (MDS) depicting the relatedness of subtidal macroalgal assemblages (using species presence) among SW (Hamelin Bay), RECH (Recherche Archipelago) and FRANCIS (Isles of St Francis).

richness from Isles of St Francis to Hamelin Bay is similar. The majority of the replacement is a switch from southern temperate species to endemic south western species to more prevalence of subtropical species suggesting an increase in influence of the Leeuwin Current from east to west. For example, subtropical and tropical species from central and northern Western Australia are a small percentage of the flora of the Recherche Archipelago. Echinoderms and decapod crustaceans show a similar east to west species replacement with little change in species richness (O'Hara & Poore 2000).

How can we account for the pattern in species replacement at local and regional scales across southern Western Australia? The contemporary Leeuwin Current aids in dispersal of tropical and subtropical species to the southern coast of Western Australia, depresses upwelling resulting in high ambient light conditions at depth and reduces the seasonal variation in nearshore seawater temperatures. Yet diversity of marine organisms as demonstrated by benthic algae in this study, and echinoderms and decapod crustaceans by O'Hara & Poore (2000) is not solely driven by contemporary processes alone. Historically the influence of warmer waters further south in temperate Australia has resulted in high diversity, endemism and local species replacement.

The long term effect of the northward drifting Australian continent and the moderating effect of the warm Leeuwin Current have resulted in a diverse and highly endemic marine macroalgal flora (Phillips 2001). Isolation can explain the endemism but what historically has produced and maintained the diversity? High local species replacement is a signature of the benthic macroalgae of this region (Kendrick *et al.* 1999, 2004; Goldberg & Kendrick 2004; Toohey *et al.* 2007). Wernberg *et al.* (2003) found 33% of nested variation in species richness was accounted for by local species turnover. Similarly, Goldberg & Kendrick (2004) found approximately 60% of all macroalgal species found in a detailed survey of 6 islands in the western Recherche Archipelago were rare, occurring as less than 5 gm wet weight across 216 quadrats where the average algal biomass from the quadrats was 1kg or more. Sixty percent of 220 macroalgal species accounted for this local scale species replacement. Kendrick *et al.* (1999) reported that similar high local species replacement, or turnover, was not accounted for by differences between reefs and exposure to ocean swells at Marmion, on the west coast of Western Australia.

What drives local species replacement? This is not associated with any broad scale oceanographic gradients but to the successful colonisation and maintenance of small local populations. What aspect of this marine environment is so unique that it has historically promoted and in contemporary time scales maintained such high alpha, or local diversity? Ecological theory about species coexistence suggests a series of interrelated processes support the high species turnover we have observed. Firstly, competitive networks can be decoupled and the major factor usually invoked is the frequency and extent of biological and physical disturbances. Competitive networks may also not be established if the assemblages are not density-dependent.

Macroalgal species can produce up to millions of reproductive propagules per thallus (Kendrick & Walker 2005), although dispersal is thought to be limiting as propagules have a small planktonic lifespan. Successful dispersal and recruitment into a density-independent adult population can result in decoupling of competition and the co-existence of many species. The stochastic nature of disturbance and recruitment temporally and spatially can also result in patchy spatial distribution of species, especially when associated with highly competitive species like the kelp *Ecklonia radiata*, common on temperate coasts of Western Australia. The frequency and size of the gap creating disturbance and time of recolonization of gaps in kelp forests determines the biomass and species richness of macroalgae in the assemblage (Toohey *et al.* 2007). Once competition from the kelp is reduced the number of species colonising the reef increases dramatically although the biomass of the assemblage is small. As the kelp recolonises the gaps species richness declines and overall biomass increases (Toohey *et al.* 2007).

The realized niche concept is poorly identified for marine benthic flora and fauna although much of the observed small scale species replacement may be driven by very fine scale differences in the reef that affect what species colonise it (Toohey & Kendrick 2008). Recent work on the effect of reef topography on assemblage structure and diversity of macroalgae has demonstrated that competitive interactions on complex reefs can be reduced and diversity increased through increasing niches and through niche overlap for foliose algae. Rugose, topographically complex reefs affect the strength and direction of competition by *Ecklonia radiata* (Toohey & Kendrick 2008). This spatial complexity enhances the number of species associated with kelp forests, whereas in a topographically poor planar reef the negative effect of kelps on the colonisation and persistence of other macroalgae is more evident (Kendrick *et al.* 1999; Toohey *et al.* 2007).

Other canopy forming macroalgae do not show similar competitive dominance. Goldberg (2007) demonstrated that patterns in algal colonisation under canopies of *Cystophora* and *Sargassum* in the Recherche Archipelago were maintained by processes other than competition with the canopy species. Clearly the effect of canopy can be uncoupled either by the release from competition via disturbance, provision of niches through reef rugosity or through mechanisms other than direct competition by canopy species.

Historically, the species rich benthic flora and fauna have persisted on the southern coast of Western Australia because it evolved in geographical isolation, has not suffered major extinction events, glaciation in recent geological past (Holocene) nor major shifts in currents since the Eocene (McGowran *et al.* 1997). Valdovinos *et al.* (2003) demonstrated that regional context and history defines the distribution and abundance of southern temperate Pacific molluscs. Their explanation for higher mollusc biodiversity in cold temperate waters than subtropical and tropical waters was the combined effects of increased continental shelf surface area, refugia during glaciation events and the divergence of species through geographical isolation associated with historical and present currents. Similarly, the lagoonal environments reported from benthic foraminifera assemblages during the late interglacial period (Li *et al.* 1999) suggest that benign environments for marine organisms have existed at least into the recent geological past. We report algal species replacement but no real change in species richness from east to west along the south-western Australian continental shelf. Hamelin Bay in the southwestern tip of Western Australia has an assemblage of algae distinct from that of the Recherche Archipelago, and the Isles of St Francis at the eastern extent of the Great Australian Bight. This rate of species replacement, or turnover, over 18 degrees of longitude in southern Australia has already been reported for decapod crustaceans (O'Hara & Poore 2002). Their explanation hinges on both global isolation and regional connectance of species across the whole southern temperate continental shelf over the last 80 million years, combined with warming of waters as Australia has moved northward resulting in isolation and extinction of some species and southward moving warm water currents from the tropics on both the western and eastern coasts of Australia bringing warm temperate, subtropical and tropical species into more temperate latitudes. Local species replacement (alpha diversity) is extremely high in seaweed assemblages and we list what we believe are important local processes that have led to this situation. Similarly, Huston (1999) defines local processes (and their interaction with regional processes) in the evolution of diverse groups of organisms. He emphasizes the need for greater understanding of species niche concept and scaling studies of patterns in distribution and abundance such that they are sampled across scales that are relevant to the processes that have defined the survival and evolution of organisms. In benthic algae, local species turnover appears to be associated with release from competitive hierarchies, physical disturbance, high levels of recruitment and broad niche requirements.

In temperate Western Australia, historical and contemporary processes have resulted in a globally important, speciose endemic hotspot for marine flora and fauna. The Leeuwin Current has played a major but not an exclusive role in the evolution and persistence of this flora and fauna along the southern coast of Western Australia.

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